15. Millerd, A., Bonner, J. and Biale, J. B. The climacteric rise in fruit respiration as controlled by phosphorylative coupling. Plant Physiol. 28: 521–531. 1953.

16. Ohmura, T. Oxidative phosphorylation by a particulate fraction from green leaves. Arch. Biochem. Biophys. 57: 187–194. 1955.

17. Plaut, G. W. E. and Plaut, K. A. Oxidative metabolism of heart mitochondria. Jour. Biol. Chem. 199: 141–151. 1952.

18. Slater, E. C. and Holton, F. A. Oxidative phosphorylation coupled with the oxidation of α-ketoglutarate by heart-muscle sarcosomes. Biochem. Jour. 56: 28–40. 1954.

EFFECTS OF A SERIES OF CYCLES OF ALTERNATING LOW AND HIGH SOIL WATER CONTENTS ON THE RATE OF APPARENT PHOTOSYNTHESIS IN SUGAR CANE [1,2,3]

FLOYD M. ASHTON [4]

Experiment Station, Hawaiian Sugar Planters' Association, Honolulu, Hawaii and Department of Botany and Plant Pathology, The Ohio State University, Columbus, Ohio

It has long been recognized that water is one of the reactants in photosynthesis, although of the total quantity of water absorbed by a plant only a very small percentage is utilized directly in this process. It is commonly estimated that less than one percent of the water which passes into a plant is utilized chemically in photosynthesis (17). Because of the small proportion of the water absorbed which is used directly in photosynthesis, it is generally considered that internal water deficits in the plant affect the rate of photosynthesis primarily in indirect ways. Their usually retarding effects on this process have been attributed mostly either to stomatal closure and to reduced hydration of the protoplasm in chlorenchymatous cells, or to a combination of these two effects.

The effect of moisture deficits in plants on the rate of photosynthesis has been investigated by many workers and the early work is thoroughly reviewed by Miller (18). Thoday (22) reported that turgid leaves of *Helianthus annuus* L. carried on photosynthesis ten times more rapidly than wilted leaves. Iljin (13) found that when the water content of the leaves of *Bidens tripartita* L. was reduced 43 to 44 %, the rate of photosynthesis decreased from 53 to 78 %; and in the leaves of *Phlomis pungens* Willd., a water loss of 34 % caused a reduction of 13 % in the rate of photosynthesis. Iljin also reported that recovery of the original rate of photosynthesis lagged behind the regain of turgor.

Brilliant (6), using leaves of *Hedera Helix* L. and *Impatiens parviflora* Bedd., observed that photosynthesis almost stopped when leaf moisture was reduced 41 to 63 %. Schneider and Childers (20) studied photosynthesis of single leaves of apple trees under an increasing soil moisture stress and reported that before wilting of the leaves was evident, the rate of photosynthesis was reduced 55 %. When the plants showed definite wilting, there was an 87 % reduction in the rate of photosynthesis. When water was applied to the soil, in which the wilted plants were growing, the leaves usually attained turgidity within 3 to 5 hours. The rate of photosynthesis, however, did not regain its original magnitude until 2 to 7 days after watering. In general, workers have found that any considerable fluctuation in leaf moisture is almost immediately reflected in the rate of photosynthesis. Greater than an approximately 30 % reduction in the water of leaves usually results in a decrease in the rate of photosynthesis; the greater the reduction in leaf moisture, the greater the reduction in the rate of photosynthesis. When the leaf moisture is decreased to approximately 60 % of its maximum value, the rate of photosynthesis is near zero.

Kozlowski (14) using seedlings of loblolly pine (*Pinus taeda* L.) and white oak (*Quercus alba* L.) reported that as the soil moisture decreased the rate of photosynthesis of pine decreased more rapidly than that of oak. At high light intensities there was no reduction in the rate of photosynthesis over a considerable range of soil moisture for oak.

Bordeau (3) reported that with sweetgum (*Liquidambar Styraciflua* L.) the rate of photosynthesis declined slowly at first and then rapidly as the soil moisture decreased.

Borman's (2) data indicates that with northern red oak (*Quercus borealis* Michx. f.) and blackjack oak (*Quercus marilandica* Muenchh.) seedlings the rate of photosynthesis decreased at a much more uniform rate as the availability of the soil moisture decreased.

Loustalot (16) studied photosynthesis of single leaves of pecan (*Carya illinoenis* K. Koch; syn., *C. Pecan*) trees under an increasing soil moisture stress and reported that either deficient or excessive (flooding) amounts of soil moisture resulted in sub-normal rates of photosynthesis and transpiration. The degree of depression of the rates depended upon the severity

[1] Received January 10, 1956.

[2] Published with the approval of the Director as paper No. 39 in the Journal Series of Experiment Station, Hawaiian Sugar Planters' Association, Honolulu, Hawaii.

[3] Publication No. 586, Department of Botany and Plant Pathology, The Ohio State University.

[4] Present address: Department of Botany, University of California, Davis, California.

and duration of the adverse soil condition and upon the atmospheric conditions. The plants were rooted in a soil which had a field capacity of 29 % and a permanent wilting percentage of 12 %. A decrease in the rate of photosynthesis was first noted in the afternoon of the eighth day after the last irrigation when the soil moisture had decreased to 18 %. Recovery of the original rate of photosynthesis after irrigation was rapid (2 days) for the morning rate of photosynthesis, but the afternoon rate of photosynthesis did not reach its original rate until 6 days after irrigation.

Hartt (7, 8, 9) in her studies with sugar cane, concluded that photosynthesis occurs in plants rooted in soil with the water content at or below the permanent wilting percentage, but the rate of photosynthesis is much less than in plants adequately supplied with water.

The purpose of this work is to study the effects of a series of cycles of alternating low and high soil water content on the rate of photosynthesis. Hartt (7, 8, 9), Loustalot (16), and Schneider and Childers (20) have studied the rate of photosynthesis as affected by soil moisture through only one such cycle. That is, they started with a plant rooted in soil with a water content at the field capacity, allowed the soil to dry to the permanent wilting percentage, and then added water to the soil to raise the water content back to field capacity. The rate of photosynthesis was measured throughout the cycle. In this study a cycle was repeated 5 times over a period of 71 days and the effect on the rate of photosynthesis investigated. Such a series of cycles of alternating low and high soil water contents resembles soil moisture conditions prevailing in nature and under agricultural conditions. Most plants growing under natural conditions or as agricultural crops are watered periodically during a growing season, either by natural rainfall or by irrigation. Frequently between waterings soil moisture stresses become severe and limit photosynthesis. This is particularly true in irrigated agricultural areas where the amount of water available is limited. It, therefore, appears desirable to know the effect of a series of cycles of alternating low and high soil water contents on the rate of photosynthesis as measured under experimental conditions. Such information should aid in the interpretation of the behavior of plants under natural or agricultural conditions.

Methods and Materials

The shoots of two similar potted sugar cane (*Saccharum officinarum* L., var. 37-1933) plants approximately one year of age were placed in the photosynthetic chambers (fig 1). These plants were approximately 8 feet tall and had 11 leaves each at the beginning of the experiment. Each leaf had an area of about 400 square centimeters and each plant had a total leaf area of about 4400 square centimeters throughout the experiment with new leaves appearing and old leaves dying. One of the two plants was allowed to go through a series of 5 cycles of alternating low and high soil water contents; the other plant was maintained continuously at a high soil water content and was used as a control plant. A cycle consisted of 7 days of high soil water content maintained by daily irrigations, followed by a drying period during which the soil dried to the permanent wilting percentage. There was no irrigation of the treated plant during this period which was of 6 to 8 days duration, depending on environmental conditions. The high soil water content was maintained by saturating the soil with water daily at 3:30 P.M., and the low soil water content was approximately the permanent wilting percentage. Measurements were made of the rate of photosynthesis, the soil water content, and the CO_2 concentration of the air. The term, photosynthesis, as used throughout this paper refers to apparent photosynthesis, i.e., to photosynthesis minus respiration.

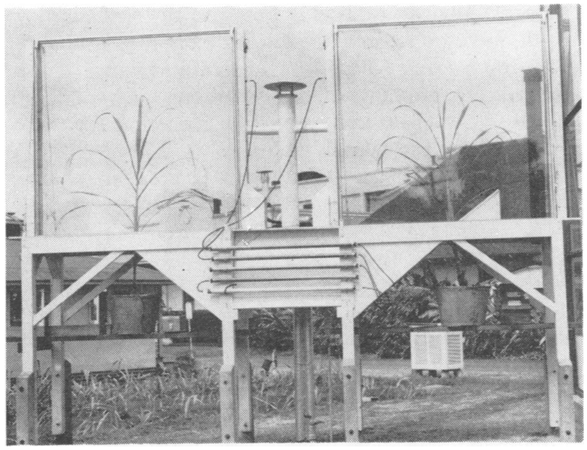

FIG. 1. Photosynthetic chambers as seen in side view.

The soil used was Manoa, a loam soil of volcanic origin, which had previously been air dried, screened through a one-eighth-inch mesh screen. Sixteen-inch pots were filled with the soil to a depth of 10 inches. A single-eye seed piece of sugar cane was planted at a two-inch depth in each pot of soil. The year preceding the photosynthesis study, the soil was fertilized to prevent mineral element deficiencies and a high soil water content was maintained by a daily watering.

The photosynthesis measurements were made batchwise in contrast to a method of continuous air flow. Most experimenters (1, 10, 11, 16, 20, 23) in the past have used a continuous flow of air through the photosynthesis chambers. In a batch method, the atmospheric air is drawn into the photosynthetic chamber in sufficient volume to displace all residual air with fresh air of atmospheric CO_2 content, it is allowed to remain there for a given period of time. After this period a sample of the air in the photosynthetic chamber is analyzed for CO_2. The decrease in the CO_2 content of the atmospheric air represents the amount of CO_2 removed from the air in photosynthesis. The length of the photosynthetic period varies with the size of the photosynthetic chamber, the rate of photosynthesis, and the total leaf area. In this investigation each photosynthetic period was 13 minutes long. The advantage of the batch method of measuring photosynthesis is that the rates of air flow do not have to be measured. Precise measurements of the rates of air flow for the large volumes of air required for a plant of this size are very difficult. Wet test meters do not have sufficient capacity to be used for such a purpose. Some investigators (10, 22) have used anemometers for the measurement of flow rates of large volumes of air through photosynthetic chambers. It is the opinion of the author that greater precision in the measurement of the rate of photosynthesis of large plants can be obtained by using the batch method for measuring the rate of photosynthesis than by using a continuous flow of air through the chambers.

Each cycle was started by drawing adequate atmospheric air through the chambers for 1 minute to completely remove all residual air. The air entered through port A (fig 2), flowed into the photosynthetic chamber via ports GG . . . , and across the chamber, exiting via ports GG . . . and port B which was connected to the blower. The hinged flutter valves FF were opened by the force of the air stream and closed by their own weight when the air stream stopped. After 1 minute the movement of air through the chambers was stopped and the photosynthetic period started. Fourteen minutes after the start of the cycle the atmospheric air was again drawn through the chambers for 1 minute in adequate volume to completely remove all residual air, thus completing one photosynthetic period and starting the next. There was no entry of air into the photosynthetic chambers during the photosynthetic period. The movement of air through the chambers during these one-minute blow-out periods was accomplished by a blower rated at a capacity of 935 ft^3/min of free air flow. The internal dimensions of each photosynthetic chamber were $72 \times 72 \times 4$ inches and its total volume was 12 ft^3. The air in each chamber was continuously recirculated by a fan (C) which blew the air through a heat exchanger (D) which cooled the air and prevented excessive temperatures. Cold water (38 to 40° F) was continuously circulated through the heat exchangers. Measurements of the rate of air flow through the heat exchangers were made and from these figures it was calculated that the air in each chamber was completely recirculated every 2 minutes. The maximum temperature in the chambers never exceeded 40° C at the end of the photosynthetic period. The minimum temperature in the chambers at the beginning of the photosynthetic period was the same as the outside air. These temperatures did not visually appear to damage the plants.

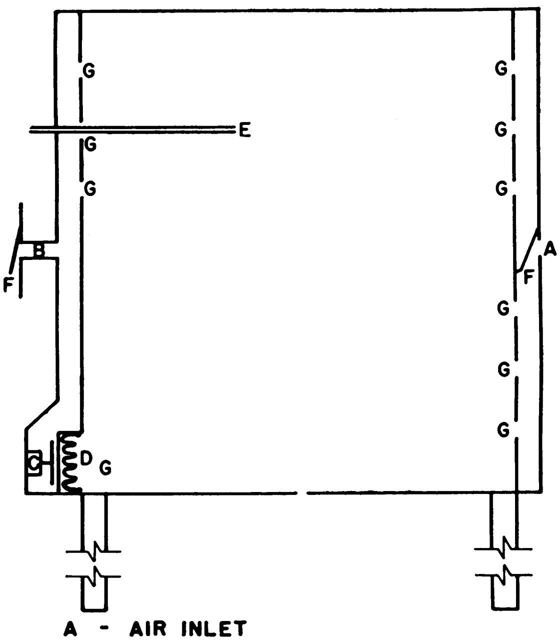

FIG. 2. Cross-sectional diagram of photosynthetic chamber.

A measurement of the CO_2 concentration of the air in each chamber was made every half hour from one hour before sunrise to one hour after sunset. Measurements of the CO_2 concentration of the atmospheric air and of the CO_2-free air were also made every half hour. CO_2-free air was prepared by passing atmospheric air through a 4-ft glass tube filled with soda lime. The air sample from the photosynthetic chambers was collected during a 5-minute period starting 9 minutes after flushing by the blower. The first 3 minutes of air flow was required for washing out the previous sample from the sampling tubes and instrument absorption cell so that only the latter portion of the 4-minute fraction of the air sample was used for CO_2 analysis. The 4-minute part of the air sample remained in the absorption cell of the spectrophotometer for 5 minutes and was used to determine the CO_2 concentration of the air from which the rate of photosynthesis was calculated. This air sample represented the air which had been in the photosynthetic chambers for 13 minutes. The 4- to 5-minute part of the air sample remained in the sampling tubes and was washed out by the next sample.

The sampling system was automatically controlled by a cycle timer and solenoid valves. A time clock turned the apparatus on one hour before sunrise and off one hour after sunset. The air samples were pulled from the chambers and pushed through the spectrophotometer by an air pump.

The CO_2 concentrations of the various air streams were measured by passing the dry air stream through the monochromator section of a Beckman Infrared Spectrophotometer (Model IR-2) and were continuously recorded on a 50-mv Brown Electronic Recorder. The air was dried before passing through the spectrophotometer by passing it through 4-ft tubes of indicating silicagel; these were recharged daily. The

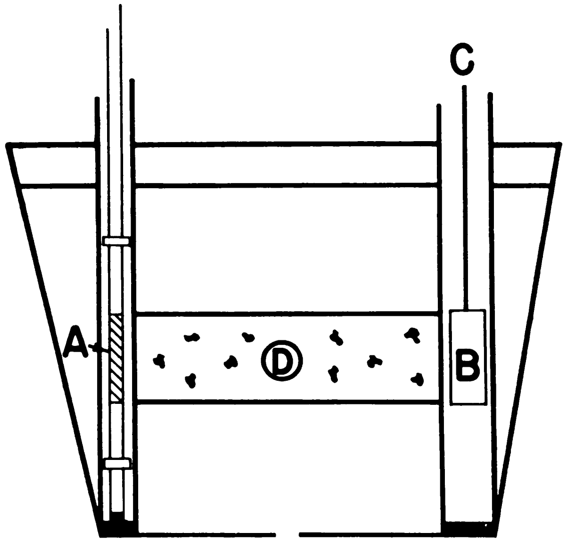

FIG. 3. Physical arrangement of the equipment for soil moisture measurements. A.—Radioactive source; B—Geiger tube; C—Electrical cable to scaler; D—Band of soil measured.

drying of the air was necessary to prevent damage to the rock salt optics of the instrument. The wave length of infrared radiation used was 4.27 μ. The instrument was calibrated by passing air of a known CO_2 concentration through it. This air of known CO_2 concentration was prepared by the addition of a pure CO_2 stream to a CO_2-free air stream. The flow rates of these two streams were determined by capillary manometric flowmeters which were built and calibrated for this purpose. The CO_2 was removed from the air by passing it through a 4-ft tube of soda lime. There was a linear relationship between the optical density and the carbon dioxide concentration from 0.00 to 0.05 % by volume under these conditions. This is in accordance with Beer's law.

In several parts of this paper a value for the percent of full photosynthesis is expressed. This is a calculated value derived by considering the CO_2 utilization of the plant growing in the soil subjected to a series of cycles of alternating low and high soil water contents as a percent of the CO_2 utilization of the plant which was continuously at a high soil water content. At the beginning of the experiment the plant subjected to a series of cycles of alternating low and high soil water contents had a slightly higher rate of photosynthesis than the plant maintained at a high soil water content. The rate of photosynthesis of the former plant was then corrected by multiplying by a factor of 0.985 which was calculated from the data of the first 8 days of the experiment when both plants were under high soil moisture conditions.

The method of Burr (Burr, G. O. Personal communication. 1953.) for the measurement of soil moisture was adapted to this study. In this method a radiation technique of measuring density is used. The basic principle involved is that the fraction of radiation absorbed in passing through a layer of matter is proportional to the density. Changes in the density of Manoa soil under the conditions of this experiment resulted almost exclusively from changes in the moisture content; therefore, this technique was satisfactory for determining soil moisture in this investigation. This method is believed to be superior to any other method now available because it is accurate through the entire soil moisture range. The physical arrangement of the equipment is illustrated in figure 3. Two plastic pipes, 1 inch and 1.5 inches inside diameter respectively, and 12 inches long, were placed vertically in the soil 8.75 inches apart. These pipes extended from the bottom of the pots to above the soil surface. The bottoms of these pipes were plugged with rubber stoppers to prevent water from entering. When measurements were not being made, the tops of these pipes were also stoppered to prevent extraneous materials from falling in. Cesium 137–Barium 137 was used as a source of gamma rays and placed at the desirable height in the 1-inch pipe during the determination. A Geiger Tube was placed in the 1.5-inch pipe at a corresponding height and the electrical leads from the tube plugged into a scaling circuit.

The Cesium 137–Barium 137 was obtained from the Atomic Energy Commission at Oak Ridge as the chloride in aqueous solution. One-fourth of a millicurie was diluted and sealed in a short piece of Tygon tubing with glass plugs. The plastic tubing was placed in an 18-inch piece of aluminum tubing. The length of this gamma ray source was 2.5 inches. This is the same length as the Geiger tube which received the radiation. This arrangement allowed a soil moisture determination on a band of soil through the center of the pot. All counts were of 5-minute duration, including a background and a standard before and after each series of measurements. The quantity of cesium selected yielded a sufficient number of counts under these conditions to give a counting error of not more than $\pm$ 1 %. Excessively high amounts

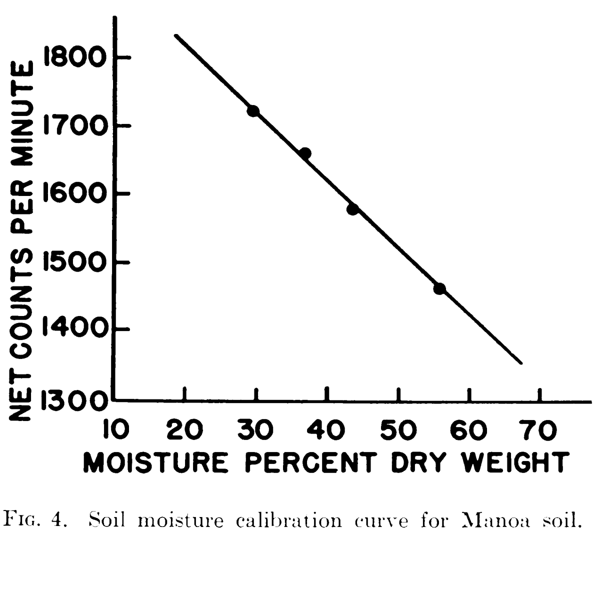

FIG. 4. Soil moisture calibration curve for Manoa soil.

of cesium were avoided to prevent harmful radiation levels to the plant, overloading the scaling circuit, and personal danger in handling. A calibration curve was drawn by plotting counts per minute against percent moisture (fig 4). The percent moisture for this calibration curve was determined by measuring soil samples from the pots at various soil water contents and oven drying the samples to a constant weight at 105° C.

The permanent wilting percentage of this soil was 24.7 % moisture on a basis of dry weight. This was measured by using sunflower as the test plant and determining the percent of moisture in the soil when the lowest pair of leaves had wilted and failed to recover turgidity after being kept in a saturated atmosphere overnight (5, 12). The percent moisture in the soil was measured by oven drying to a constant weight at 105° C. Permanent wilting percentages were also determined physiologically each time the soil reached this point during the experiment by having two sunflower plants growing in each pot with the sugar cane and confining a saturated atmosphere about the sunflower plants with a suitable chamber overnight whenever the sunflowers had wilted during the day. If the sunflower plants recovered turgidity under these conditions the soil had not reached the permanent wilting percentage. This procedure was used as a check on the soil moisture value as measured by the radiation method at this critical point of the drying cycle; the two methods were always in agreement in indicating when the soil should be irrigated.

The saturation capacity of the soil was 59.4 % moisture on dry weight basis. This was measured by placing a 12-inch column of air-dried soil in a glass tube, 1.5 inches in diameter. The bottom of this tube was closed with a one-hole rubber stopper. A small piece of glass wool was placed on top of this stopper to prevent the soil from falling out of the bottom. The amount of water which was added to this column of soil was more than enough to saturate it and the excess water drained through the glass wool and the stopper. The column of soil was allowed to drain for 72 hours before determining the percent moisture in the soil by oven drying to a constant weight at 105° C.

The field capacity of the soil was 40.7 % on a dry weight basis. This quantity was measured by a technique similar to that for saturation capacity except that the amount of water which was added to this column of soil was just enough to bring the top two-thirds of the column to field capacity; the soil in the lower part of the tube remained dry. This column of soil was undisturbed for 72 hours before determining the percent moisture in the upper two-thirds of the soil column by oven drying to a constant weight at 105° C (19, 21).

The moisture equivalent of the soil was 29.3 % on a dry weight basis. This was measured by determining the percent moisture in the soil by oven drying it to a constant weight at 105° C after the soil had been previously saturated with water and centrifuged at a force of one thousand times gravity for 30 minutes (4). In many kinds of soils the field capacity and moisture equivalent are approximately equal in value. This is not true of Manoa soil, probably because of its coarse texture (15).

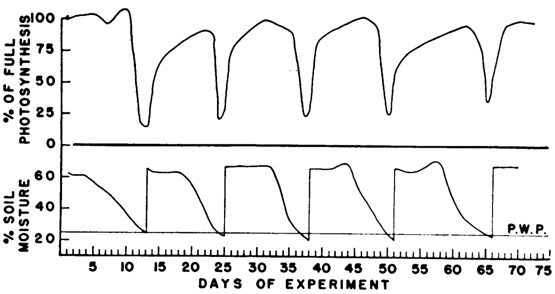

FIG. 5. Rates of photosynthesis and percentage soil moistures during 5 drying cycles.

The data presented in this paper represent the results of a single experiment. Similar results were obtained in three other experiments performed in similar fashion.

Experimental Results

GENERAL: A decrease in the rate of photosynthesis of a plant occurs when the amount of moisture in a soil in which that plant is rooted decreases from the maximum water holding capacity to the permanent wilting percentage. The rate of photosynthesis does not decrease at a uniform rate during this drying-out period. The original rate of photosynthesis is maintained until a significant soil moisture stress develops somewhere between field capacity and permanent wilting percentage and then decreases, approaching zero at the permanent wilting percentage. Several days pass after an irrigation before the plant regains the original rate of photosynthesis. This information has been known for some time from the investigations of Schneider and Childers (20) who worked with young apple trees, and Loustalot (16) who worked with young pecan trees.

During the present investigation these facts were substantiated (fig 5). The daily cumulative rate of photosynthesis was calculated by the summation of the rates of photosynthesis of the sixteen individual 30-minute photosynthetic periods, from 8:00 A.M. to 4:00 P.M. The rate of photosynthesis of each individual photosynthetic period was calculated by subtracting the CO_2 concentration (% by volume) of the air in the photosynthetic chambers at the end of the photosynthetic period from the CO_2 concentration of the atmospheric air measured during the same 30-minute period. The resulting concentration of CO_2 was converted to gms of CO_2 uptake per photosynthetic period per plant. The following formula was used for the calculation:

$$M = \Delta C \times V \times 1.977 \times 2.308$$

M = gms CO_2 uptake/30 min.

ΔC = initial conc of CO_2 minus final conc of CO_2 (CO_2 conc expressed as % by vol).

V = vol of chamber in liters.
1.977 = density of CO_2 (gms/l, S.T.P.).
2.308 = ratio, 30-min cycle/13-min photosynthetic period.

A decrease in the daily cumulative rate of photosynthesis occurred when the soil moisture was at some point below field capacity and above the permanent wilting percentage. The recovery of full photosynthesis after irrigation was slow, requiring several days. A recovery of 80 to 90 % of full photosynthesis was achieved in about 2 days. In sugar cane, therefore, as in plants previously worked with, a relatively high rate of photosynthesis is maintained until the soil moisture is at some point below the field capacity and the recovery of the original rate of photosynthesis following irrigation requires several days.

Daily Courses of Photosynthesis as the Soil Moisture Decreases to the Permanent Wilting Percentage and Recovery of Photosnythesis after Irrigation: An examination of the daily courses of photosynthesis as the soil moisture tension increases to the permanent wilting percentage and its recovery after irrigation (fig 6), reveals several significant points. These data are taken from the third cycle of alternating low and high soil moisture contents; however, results were similar in all 5 cycles. At the beginning of a drying out cycle when the daily irrigations are stopped, no significant decrease in the rate of photosynthesis takes place for a few days. There was no decrease in the rate of photosynthesis until the soil moisture decreased to some point below field capacity and above the permanent wilting percentage. No attempt is made to determine the precise soil moisture tension at which soil moisture is limiting to the process of photosynthesis. Figure 6 indicates that this point is about midway between field capacity and permanent wilting percentage under this set of conditions. However, this might not be the value under a different set of experimental conditions. The crucial factor is the internal moisture conditions of the plant rather than a specific soil moisture tension. Adverse internal moisture conditions of a plant occurs when the water losses exceed the water uptake to a significant degree. Any of a number of environmental factors or combinations of these factors may effect this critical balance.

An overnight recovery in the rate of photosynthesis occurred when the plant was under a moisture stress the previous afternoon. This was observable when the rate of photosynthesis at 4:00 P.M. two days before irrigation was compared with the rate of photosynthesis at 8:00 A.M. one day after irrigation and also when the rate of photosynthesis at 4:00 P.M. one day before irrigation was compared with the rate of photosynthesis at 8:00 A.M. the day of irrigation. This was presumably the result of an improved internal water balance in the plant.

Effect of Light Intensity on the Rate of Photosynthesis When the Sugar Cane Plant Is under a Moisture Stress: An increase in the rate of photosynthesis of sugar cane plant occurred when the soil moisture was near the permanent wilting percentage and when there was a brief period of reduced light intensity; this was probably the result of an improved water balance within the plant. This was demonstrated either when brief cloudy periods occurred or when shadows were cast on the lower leaves by the upper leaves. This later condition occurred at midday when the sun reached its daily maximum altitude.

The sixty-fourth day of the experiment, or 1 day before the soil reached its permanent wilting percentage in the fifth cycle of alternating low and high soil moisture conditions, a unique set of natural conditions occurred which demonstrated the effect of cloudiness

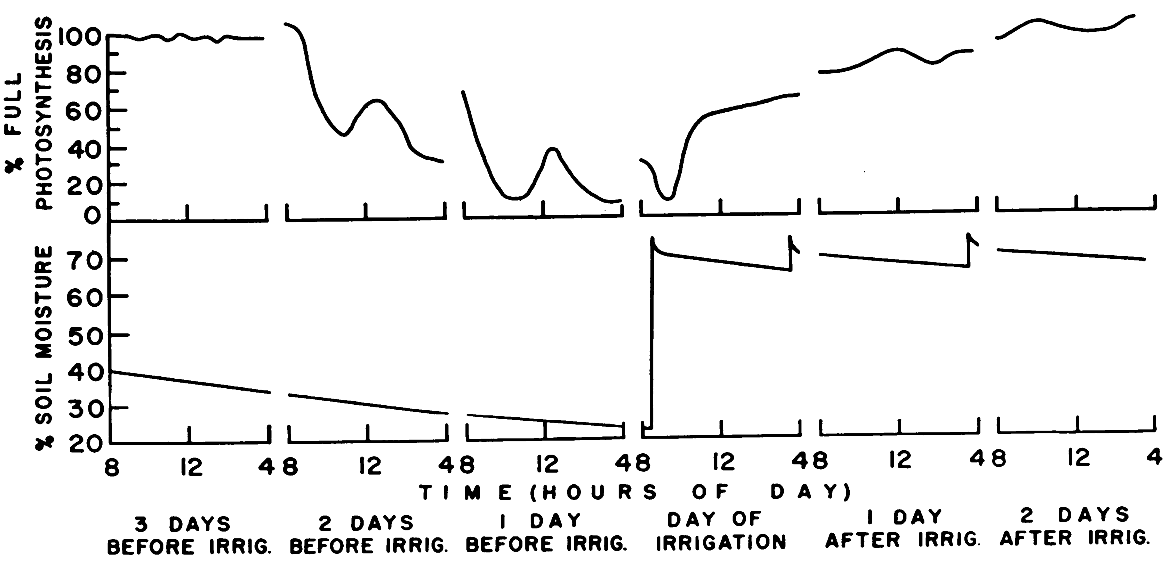

Fig. 6. Daily courses of photosynthesis as the soil moisture tension increases to the permanent wilting percentage.

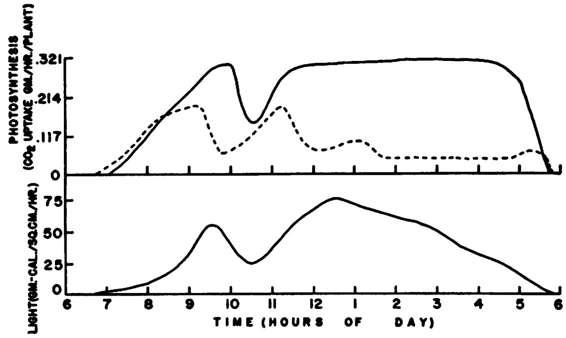

FIG. 7. The daily course of photosynthesis in relation to light intensity showing an increase in the rate of photosynthesis of a sugar cane plant under a moisture stress during a brief period of reduced light intensity. ----- plant under moisture stress, ——— control plant.

on the rate of photosynthesis of the sugar cane plant in soil near the permanent wilting percentage. No leaves were wilted at 8:00 A.M.; at 9:30 A.M., leaves 1 and 2 were wilted; at 1:00 P.M., leaves 1, 2, 3, 4 and 5 were wilted. The leaves are counted from the top down; number 1 leaf is the first leaf which is at least half unrolled. It is also the first leaf to show signs of wilt as the plant passes into a condition of internal moisture stress. The soil moisture was just above the permanent wilting percentage most of the day. It was 25 % or at the permanent wilting percentage at 3:30 P.M. The light intensity was moderately high (54.3 gm cal/sq cm × hr) from 9:00 A.M. to 10:00 A.M. followed by a period of lower light intensity (23.8 gm cal/sq cm × hr) from 10:00 A.M. to 11:00 A.M., and followed in turn by a moderately high light intensity (53.4 gm cal/sq cm × hr) from 11:00 A.M. to 12:00 noon. The light intensity values were measured by a recording pyrheliometer located about 100 yards from the experimental site. The light intensities as given are the hourly integrated values. The daily course of photosynthesis of the control plant, the plant under moisture stress, and the light intensities are presented graphically in figure 7. The rate of photosynthesis of both plants increased as usual as the light intensities increased until about 9:00 A.M. when the rate of photosynthesis of the plant under moisture stress decreased rapidly. During the period from 10:00 A.M. to 11:00 A.M., during which the light intensity decreased to a low value, the rate of photosynthesis of the control plant decreased while that of the plant under moisture stress increased. This increase in the rate of photosynthesis of the latter plant presumably results from a decrease of the moisture stress during this period of low light intensity. When the light intensity again increased, the rate of photosynthesis of the control plant increased while that of the plant under the moisture stress decreased. This same type of recovery was again noted slightly after midday and again in the late afternoon. The midday recovery resulted from somewhat lower light intensities than the maximum as a result of the shading of the lower leaves by the upper leaves. The midday light intensity was not low enough to limit the rate of photosynthesis of the control plant. The late afternoon recovery of the rate of photosynthesis of the plant in soil near the permanent wilting percentage resulted from naturally occurring low light intensities.

The data from the forty-ninth day of the experiment, or 2 days before the soil reached its permanent wilting percentage in the fourth cycle of alternating low and high soil moisture conditions, is a good example of midday recovery of the rate of photosynthesis of the sugar cane plant in a soil near the permanent wilting percentage. It also illustrates the close relationship between the severity of wilting and the rate of photosynthesis of the plant under study. In figure 8, the daily courses of photosynthesis of the control plant and of the plant under moisture stress are presented graphically, together with the daily cycle of light intensities. The soil moisture was above the permanent wilting percentage during the entire day, being 27 % at 3:30 P.M. The rate of photosynthesis of both plants increased as usual as the light intensity increased until about 9:00 A.M. The rate of photosynthesis of the plant in soil near the permanent wilting percentage decreased after 9:00 A.M. to a minimum at about 11:00 A.M., after which it increased to a maximum at about 12:30 P.M. A minimum was again reached a little after 3:00 P.M., and a maximum was again reached a little after 4:00 P.M. The decline in the rate of photosynthesis after this second maximum coincides with the late afternoon decrease in light intensity. The severity of wilting was as follows: 8:00 A.M., no wilting; 9:00 A.M., leaf 1 wilted; 10:00 A.M., leaves 1, 2, 3, 4 and 5 wilted; 11:00 A.M., leaves 1, 2, 3, 4 and 5 wilted; 12:00 noon, no wilting; 1:00 P.M., leaves 1, 2, 3, 4 and 5 wilted; 2:00 P.M., leaves 1, 2, 3, 4 and 5 wilted; 3:00 P.M., leaves 1, 2, 3, 4 and 5 wilted; 4:00 P.M., no wilting. The rate of photosynthesis was at a maximum when little wilting was evident and the rate of photosynthesis was at a minimum when wilting was most severe.

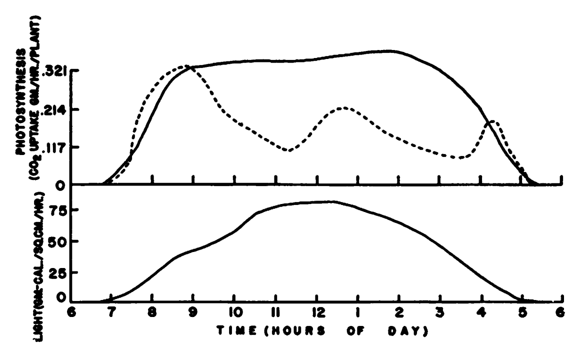

FIG. 8. The daily course of photosynthesis in relation to light intensity showing the midday recovery of the rate of photosynthesis of a sugar cane plant under a condition of internal moisture stress. ----- plant under moisture stress, ——— control plant.

THE EFFECTS OF A SERIES OF CYCLES OF ALTERNATING LOW AND HIGH SOIL WATER CONTENTS ON THE RATE OF PHOTOSYNTHESIS: The over-all results of this phase of the experiment are presented graphically in figure 5. The photosynthetic values are the cumulative daily values of the sixteen individual 30-minute photosynthetic periods from 8:00 A.M. to 4:00 P.M. The soil moisture determinations were made between 3:00 P.M. and 3:30 P.M. daily.

The percent of photosynthesis relative to the control plant on the day of irrigation in each of the five cycles is presented in figure 9. The rate of photosynthesis on all 5 days was less than that of the control plant. The plant under moisture stress was irrigated at 8:30 A.M. There were two trends in the rate of photosynthesis on the day of irrigation which changed progressively as the cycles of alternating low and high soil moisture progressed from the first to the fifth cycle. The first trend was the shortening of the period of time after irrigation before the first increase in the rate of photosynthesis was noted. In the first cycle, this period of time was 3 hours; in the second cycle 2.5 hours, in the third cycle 1.5 hours, in the fourth cycle 1.5 hours, and in the fifth cycle 0.5 hour. The speed at which the sugar cane plant shows signs of recovery in the rate of photosynthesis following irrigation of a soil which has reached the permanent wilting percentage increased as the cycles of alternating low and high soil moistures progressed from the first to the fifth cycle. Also the daily cumulative rate of photosynthesis the day of irrigation progressively increased as the alternating cycles of low and high soil moisture progressed from the first to the fifth cycle. This can be observed in figure 9, but is clearer in figure 10 where photosynthetic rates are presented as the daily cumulative values. In the first cycle, the rate of photosynthesis was actually less on the day of irrigation than it was on the preceding day, the actual value being only 14 % of the control plant. In the second cycle this value was 32 %, in the third cycle 44 %, in the fourth cycle 59 %, and in the fifth cycle 60 %. These data also illustrate the increasing rate of recovery of photosynthesis of the sugar cane plant following irrigation of a soil at the permanent wilting percentage as the number of cycles of alternating low and high soil water contents increases. The soil water content of the soil on these 5 days was 23, 23, 20, 20, and 23 %, respectively, just prior to irrigation at 8:00 A.M. to 8:30 A.M.

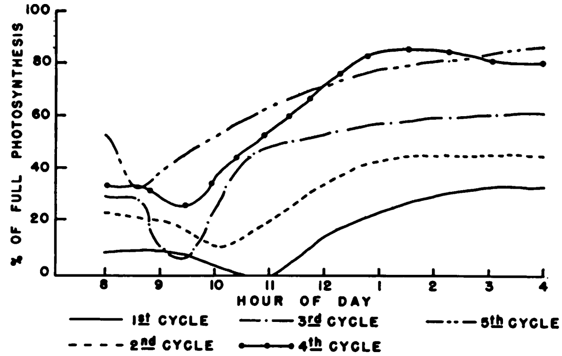

FIG. 9. The percent of photosynthesis relative to the control plant on the day of irrigation.

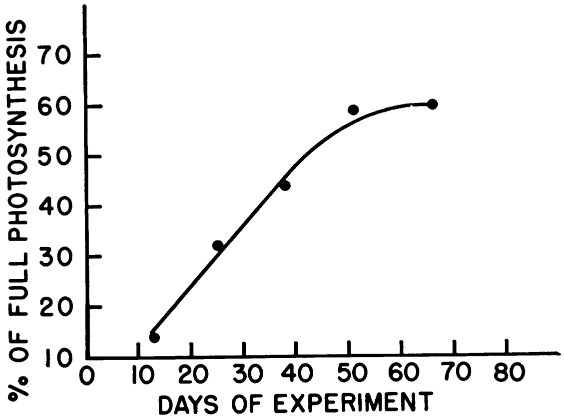

FIG. 10. The daily cumulative rate of photosynthesis on the day of irrigation. (Points on curve correspond to days of irrigation.)

SUMMARY

An investigation of the effects of a series of cycles of alternating low and high soil water contents on the rate of apparent photosynthesis has been conducted with sugar cane (*Saccharum officinarum* L., var. 37-1933) plants. A shoot of each of two similar potted plants approximately one year of age was placed in a photosynthetic chamber. One of the two plants was allowed to go through a series of five cycles of alternating low and high soil water contents; the other plant was maintained at a high soil water content and was used as a control plant. The high soil water content was maintained by thoroughly watering the soil daily, and the low soil water content was approximately the permanent wilting percentage. The rate of apparent photosynthesis of each plant was determined once every half hour by measuring the amount of CO_2 removed from the air after a 13-minute photosynthetic period. The CO_2 concentrations were measured by a recording infrared spectrophotometer. The measurement of the soil moisture was made by using a radiation technique of measuring soil density. The basic principle involved is that the fraction of radiation absorbed in passing through a layer of matter is proportional to the density. Changes in the density of Manoa soil under the conditions of this experiment resulted almost exclusively from changes in the moisture content.

There was a progressive increase in the daily cumulative rate of photosynthesis, as the cycles of alternating low and high soil water contents progressed from the first to the fifth cycle, on the day of irrigation, on the first day after irrigation, and on the second day after irrigation. The increase became progressively less marked on the latter two days and was not clearly apparent on the third day after irrigation. There was also a progressive decrease in the interval of time before the sugar cane plant showed the first increase in the rate of photosynthesis following irrigation as the cycles of alternating low and high soil water contents progressed from the first to the fifth cycle.

An over-night recovery in the rate of photosynthesis occurred even when the soil water content was at the permanent wilting percentage.

An increase in the rate of photosynthesis of the plant in soil near the permanent wilting percentage occurred when there was a brief period of reduced light intensity, but did not occur when the water supply was adequate. This was evident when a brief cloudy period occurred or when shadows were cast on the lower leaves by the upper leaves, a condition which occurred at midday when the sun reached its daily maximum height.

The writer wishes to express his sincere appreciation to Dr. Bernard S. Meyer and Dr. George O. Burr for their guidance and helpful criticism throughout the course of this investigation. The writer also wishes to express his gratitude to the Experiment Station Committee and Director of the Experiment Station of the Hawaiian Sugar Planters' Association for the support of this investigation.

Literature Cited

1. Böhning, R. H. Time course of photosynthesis in apple leaves exposed to continuous illumination. Plant Physiol. 24: 222–240. 1949.
2. Borman, F. H. Factors determining the role of loblolly pine and sweetgum in early old-field succession in the Piedmont of North Carolina. Ecol. Monographs 23: 339–358. 1953.
3. Bordeau, P. Oak seedling ecology determining segregation of species in Piedmont oak-hickory forests. Ecol. Monographs 24: 297–320. 1954.
4. Briggs, L. J. and McLane, J. W. The moisture equivalent of soils. U. S. Bur. Soils, Bull. 45. 1907.
5. Briggs, L. J. and Shantz, H. L. The wilting coefficient for different plants and its indirect determination. U. S. Dept. Agr. Bur. Plant Industry, Bull. 230. 1912.
6. Brilliant, B. Le teneur en eau dans les feuilles et l'energie assimilatrice. Comp. rend. acad. sci., France 173: 2122–2125. 1924.
7. Hartt, C. E. Water and cane ripening. Hawaiian Sugar Planters' Record 38: 193–206. 1934.
8. Hartt, C. E. Further notes on water and cane ripening. Hawaiian Sugar Planters' Record 40: 355–381. 1936.
9. Hartt, C. E. The third study of water and cane ripening. Hawaiian Sugar Planters' Record 43: 145–158. 1939.
10. Heinicke, A. J. and Childers, N. F. The daily rate of photosynthesis, during the growing season 1935, of a young apple tree bearing age. Agr. Expt. Sta., Cornell Univ., Mem. 201. 1937.
11. Heinicke, A. J. and Hoffman, M. B. The rate of photosynthesis of apple leaves under natural conditions. Part I. Agr. Expt. Sta., Cornell Univ., Bull. 577. 1933.
12. Hendrickson, A. H. and Veihmeyer, F. J. Irrigation experiments with peaches in California. Agr. Expt. Sta., California, Bull. 479: 3–56. 1929.
13. Iljin, W. S. Der Einfluss des Wassermangels auf die Kohlenstoffassimilation duren die Pflanzen. Flora 116: 360–378. 1923.
14. Kozlowski, T. T. Light and water in relation to growth and competition of Piedmont forest tree species. Ecol. Monographs 19: 207–231. 1949.
15. Kramer, P. J. Plant and Soil Water Relations. P. 36. McGraw-Hill Book Co., New York 1949.
16. Loustalot, A. J. Influence of soil moisture conditions on apparent photosynthesis and transpiration of pecan leaves. Jour. Agr. Research 71: 519–532. 1945.
17. Meyer, B. S. and Anderson, D. B. Plant Physiology, 2nd ed. P. 356. D. Van Nostrand Co., New York 1952.
18. Miller, E. C. Plant Physiology, 2nd ed. Pp. 598–599. McGraw-Hill Book Co., New York 1938.
19. Olmstead, L. B. Some moisture relations of the soils from the erosion experiment stations. U. S. Dept. Agr., Tech. Bull. 562. 1937.
20. Schneider, G. W. and Childers, N. F. Influence of soil moisture on photosynthesis, respiration, and transpiration of apple leaves. Plant Physiol. 16: 565–583. 1941.
21. Shan, C. F. The normal moisture capacity of soils. Soil Sci. 23: 303. 1927.
22. Thoday, D. Experimental researches on vegetable assimilation and respiration. VI. Some experiments on assimilation in the open air. Proc. Roy. Soc. (London) B. 82: 421–450. 1910.
23. Thomas, M. D. and Hill, G. R. Photosynthesis under field conditions. In: Photosynthesis in Plants, J. Franck and W. E. Loomis, eds. Pp. 19–52. The Iowa State College Press, Ames, Iowa 1949.